

## Anatomical Studies of the Neotropical Cyatheaceae. II. Metaxya and Lophosoria

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The classification of the monotypic tree fern genera *Metaxya* and *Lophosoria* has undergone several revisions. Early taxonomists placed these genera, with the dicksonioid group, in the family Cyatheaceae (Diels, 1902; Christensen, 1906; Maxon, 1912). Bower (1926) stressed the importance of soral position and placed these primitive genera in the family Protocyatheaceae. Later workers (Christensen, 1938; Copeland, 1947) included the two genera in the Cyatheaceae, but excluded the dicksonioid group from that family. Based upon morphological, developmental and anatomical data, Holttum and Sen (1961) again placed *Metaxya* and *Lophosoria* and the dicksonioid ferns into the single family Cyatheaceae. More recently, Tryon (1970) revised the classification of the Cyatheaceae, excluding members of the Dicksoniaceae. He recognized *Metaxya* and *Lophosoria* as distinctive genera and placed them in an independent position at the base of his phyletic scheme for the family.

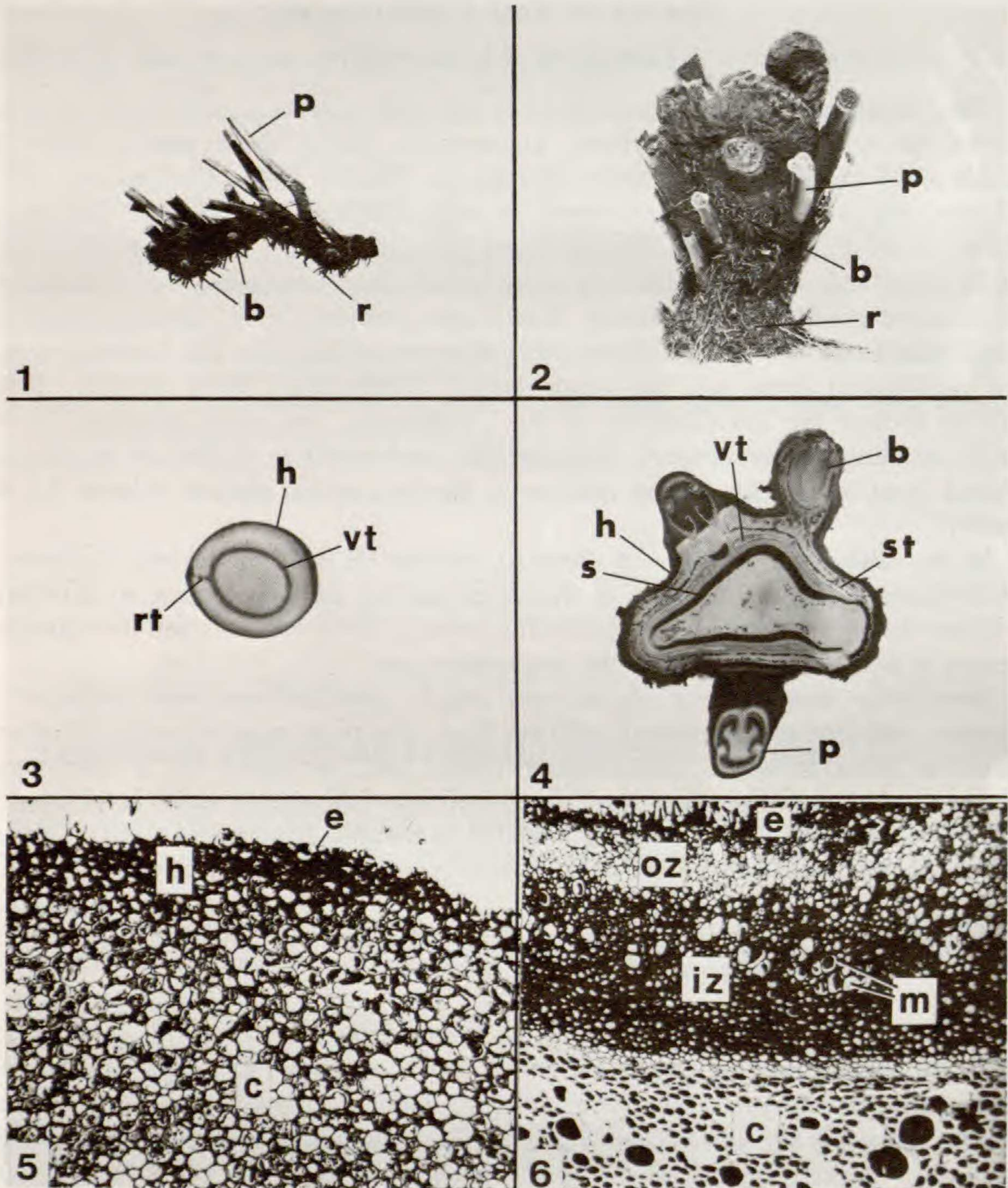
In this study, the anatomy of *Metaxya rostrata* (H.B.K.) Presl and *Lophosoria quadripinnata* (Gmel.) C. Chr. is elucidated and an attempt is made to determine whether the proposed phyletic relationship between these two taxa and the squamate genera of tree ferns is supported by anatomical data.

Developing shoot tips of *M. rostrata* and *L. quadripinnata* were collected in montane and lowland rainforests in Costa Rica. The plant materials were killed and fixed in formalin-acetic acid-alcohol (FAA) and sectioned on a macrotome (Lucansky, 1976a). The slices were partitioned into manageable sizes, dehydrated in a tertiary-butyl alcohol series and embedded in paraffin (Johansen, 1940). Sections (10  $\mu\text{m}$ ) were made and stained in a safranin-fast green series. Stained sections were photographed with a Nikon M-35S camera, whereas entire slices were photographed with a Pentax 35 mm single lens reflex camera. Voucher specimens are deposited in the herbarium of Duke University.

### RESULTS AND DISCUSSION

Based upon stem and petiole indument, nodal patterns, and vascular anatomy, *Metaxya* and *Lophosoria* are similar and represent distinctive and primitive genera in the neotropical Cyatheaceae (Lucansky, 1974a; Lucansky & White, 1974). Both genera are characterized by unbranched, multicellular trichomes on both the rhizome (stem) and petioles. *Metaxya rostrata* possesses a prostrate, dorsiventral rhizome, whereas a short, upright radial stem occurs in *Lophosoria quadripinnata* (Figs. 1 and 2). The presence of trichomes and a procumbent habit are considered primitive characters in the Cyatheaceae (Bower, 1913). The squamate genera of the New World tree ferns have an arborescent habit, except for an acaulescent habit in *Cnemidaria* (Tryon, 1970). *Metaxya* has once-pinnate leaves inserted laterally and dorsally on the rhizome, whereas *Lophosoria* has decomposed leaves inserted over

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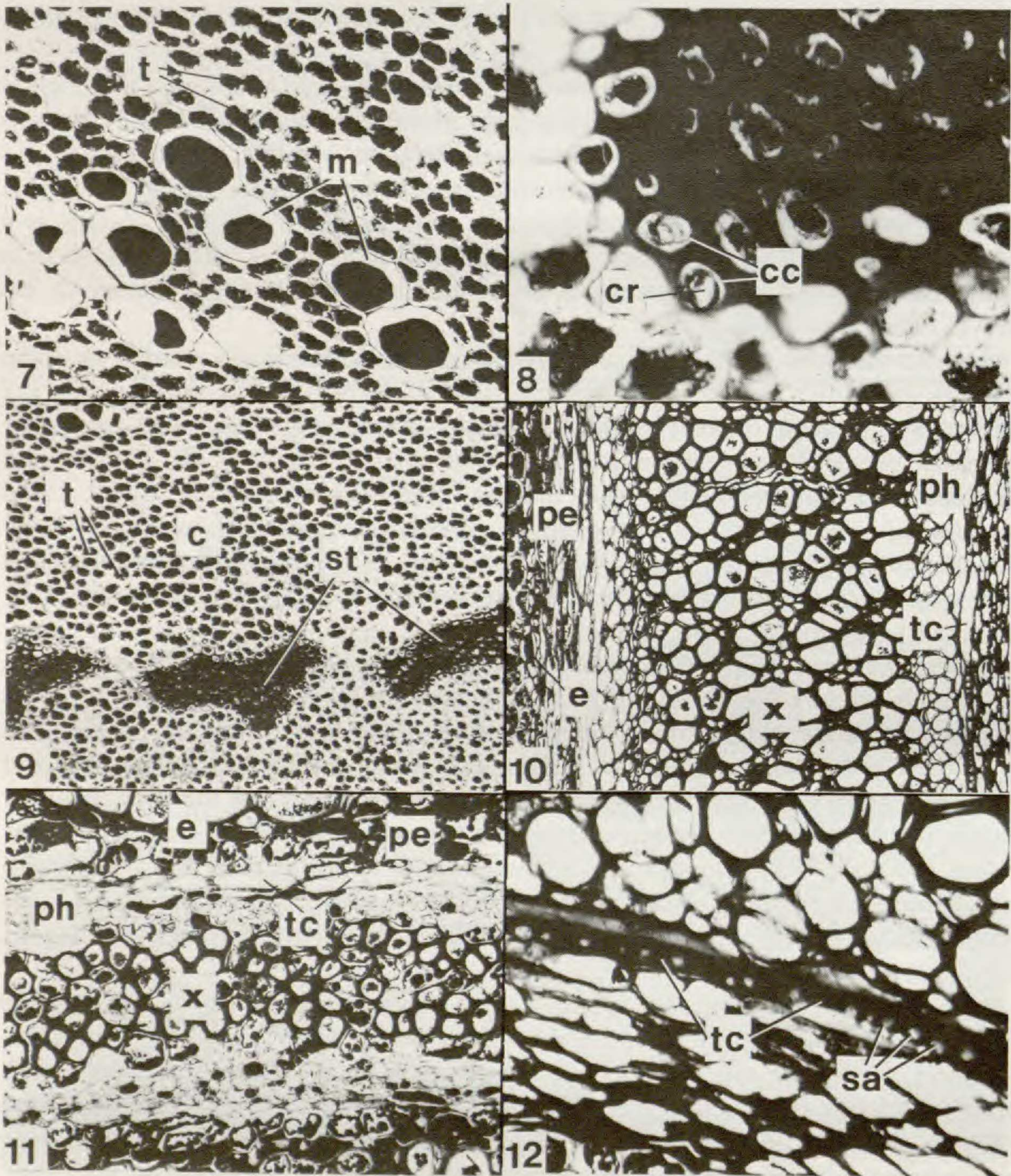
FIGS. 1-6. Habit, transections, and anatomical details of tree fern stems. FIG. 1. Prostrate rhizome of *Metaxya rostrata*,  $\times 0.5$ . Note adventitious buds. FIG. 2. Short, upright stem of *Lophosoria quadripinnata*,  $\times 0.6$ . FIG. 3. Transection of rhizome (amphiphloic siphonostele) of *M. rostrata*,  $\times 1.7$ . FIG. 4. Transection of rhizome (dictyostele) of *L. quadripinnata*,  $\times 0.4$ . FIG. 5. Hypodermis of *M. rostrata*,  $\times 54$ . FIG. 6. Two-zoned hypodermis of *L. quadripinnata*,  $\times 57$ . The abbreviations are: b = adventitious bud, c = cortex, e = epidermis, h = hypodermis, iz = inner zone, m = mucilage-sac cell, oz = outer zone, p = petiole, r = adventitious roots, rt = root trace, s = stellar sheath, st = sclerenchyma tissue, and vt = vascular tissue.

the entire surface of the stem. Adventitious roots arise from the leaf bases, buds and stems of both species (*Figs. 1 and 2*). While much is known morphologically about these two genera, comparative anatomical data are almost totally lacking for these neotropical species.

Both *Metaxya* and *Lophosoria* have an amphiphloic siphonostele, although a dictyostelic pattern with overlapping leaf gaps frequently occurs in *L. quadripinnata* (*Figs. 3 and 4*). Bower (1912) found no such stelar pattern in this species, but did indicate an approach to dictyostely in some specimens. No dictyostelic pattern is observed in *Metaxya*. The siphonostelic axis devoid of overlapping leaf gaps is a relatively primitive feature in the Cyatheaceae, and according to Holttum (1965), a siphonostelic, dorsiventral rhizome is an evolutionary development related to the growth habit of the plant.

Stem transections of *Metaxya* and *Lophosoria* are anatomically similar in some respects, but differ in certain anatomical features. In both genera, a single-layered epidermis composed of thick-walled, variously shaped cells filled with tannins is generally persistent in the mature sporophyte (*Figs. 5 and 6*). In *Culcita* and *Cystodium*, the outer epidermal walls may be either thickened (Sen & Mitra, 1966) or cutinized (Sen, 1968). In the squamate genera, the epidermal layer is typically sloughed off in the mature plant (Lucansky, 1976b, 1977), although remnants of this layer may persist. Beneath the epidermis in *Metaxya* is a hypodermis composed of sclerified parenchyma cells filled with tannins and infrequently starch grains (*Fig. 5*), whereas a two-zoned hypodermis is found in *Lophosoria* (*Fig. 6*). The outer zone (8–10 cells thick) is composed of thick-walled parenchyma cells filled with tannin droplets; the inner zone (20–25 cells) consists of smaller, sclerified parenchyma cells filled with tannins. Groups of large mucilage-sac cells are randomly scattered within this latter zone (*Fig. 6*). Previous workers had reported that the hypodermis of certain tree fern species consists solely of sclerenchymatous fibers (Ogura, 1938; Mehra & Singh, 1955); however, the squamate genera typically possess a two-zoned hypodermis composed of thick-walled parenchyma cells and sclerified parenchyma cells (Lucansky, 1976b, 1977). Except for *Metaxya*, a two-zoned hypodermis is characteristic of the neotropical Cyatheaceae.

In *Metaxya*, the cortex is composed of large, irregularly shaped, thick-walled parenchyma cells filled with tannins and starch grains (*Fig. 5*). In older rhizomes, the cortical cells become sclerified and resemble fibers. In *Lophosoria*, the cortex consists of large, thin-walled parenchyma cells filled with tannins and starch grains, although the outermost layers may be thick-walled. Within the cortex, large mucilage-sac cells are randomly distributed, either singly or in groups of 3–15 (*Fig. 7*). Distinctive cells called cubical cells occur between the hypodermal and cortical regions in *Lophosoria* (*Fig. 8*), whereas these cells are lacking in these regions in *Metaxya*. Holttum and Sen (1961) reported only solitary cubical cells in the cortex of *Lophosoria*, but they may form a discontinuous layer. Cubical cells also occur in the cortical region of the squamate genera of the neotropical Cyatheaceae (Lucansky, 1976b, 1977) and are found in the cortex of certain dicksonioid species (Sen, 1964). These distinctive cells usually contain a single, large, irregularly shaped crystal that is thought to be composed of silica (Sen, 1968). Although Ogura (1938) thought that



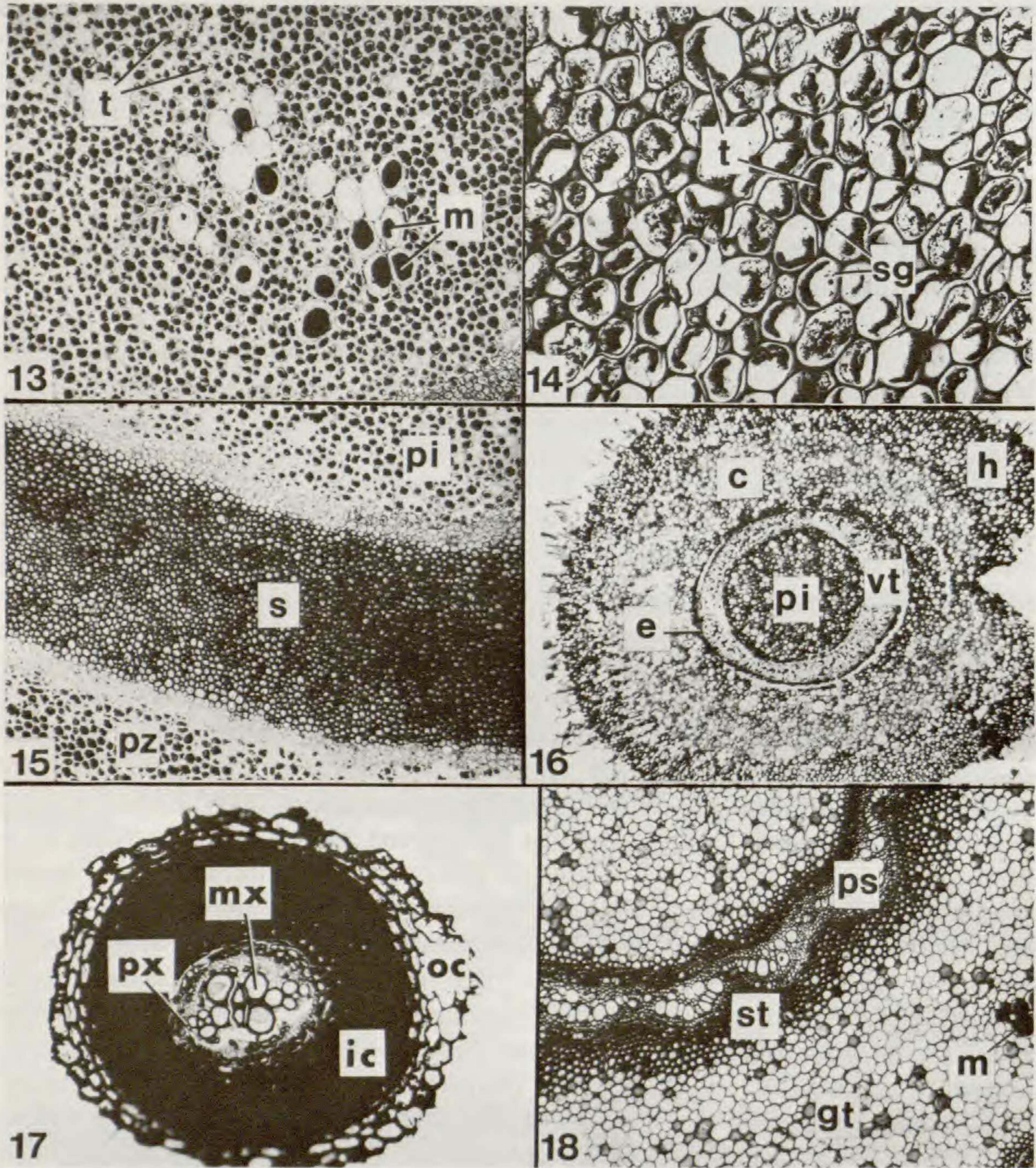
FIGS. 7-12. Anatomical details of tree fern stems. FIG. 7. Cortex of *L. quadripinnata*,  $\times 127$ . Note mucilage-sac cells. FIG. 8. Cubical cells with crystals in *L. quadripinnata*,  $\times 429$ . FIG. 9. Localized sclerenchymatous areas (dissected external stelar sheath) in cortex of *L. quadripinnata*,  $\times 50$ . FIG. 10. Meristele of *L. quadripinnata*,  $\times 124$ . Note tangential cells. FIG. 11. Tangential cells in stele of *M. rostrata*,  $\times 220$ . FIG. 12. Tangential cells with lateral sieve areas in primary phloem of *L. quadripinnata*,  $\times 464$ . The abbreviations are: c = cortex, cc = cubical cell, cr = crystal, e = endodermis, m = mucilage-sac cell, pe = pericycle, ph = phloem, sa = sieve area, st = sclerified tissue, t = tannins, tc = tangential cell, and x = xylem.

cubical cells were sclerenchyma cells, their living protoplast, wall morphology, position, and resemblance to parenchyma cells in young stems shows that they are thick-walled parenchyma. Sen's (1964) report that they were not sclerenchyma cells is based upon their rate of cell division and cellular inclusions. Also scattered in the cortex of *Lophosoria* are localized areas of sclerified tissue (transitional parenchyma-to-sclerenchyma cells) that vary in shape and size (Fig. 9). The stelar sheaths in certain squamate genera arise from the fusion of such localized areas of sclerenchyma cells (Lucansky & White, 1976), and these areas in *Lophosoria* occasionally fuse to form a dissected stelar sheath and may represent an early evolutionary stage in the development of an external stelar sheath. Localized patches of sclerenchyma tissue have also been noted in the cortical region of *Trichipteris microphylla* and *Cyathea suprastrigosa* (Lucansky, 1977) and in *Cystodium sorbifolium* (Sen & Mittra, 1966). Cubical cells filled with solitary crystals (Fig. 8) frequently occur between these sclerenchymatous areas and the thin-walled parenchyma cells of the cortex in both *Lophosoria* and certain squamate species (Lucansky, 1977). No sclerenchyma tissue and cubical cells are found in the cortical region of *Metaxya*.

Cortical bundles are a characteristic feature of certain genera and species in the Cyatheaceae (Lucansky, 1974b, 1976b, 1977), but these vascular bundles do not occur in either *Metaxya* or *Lophosoria*.

A distinct, single-layered endodermis filled with tanniferous substances delimits the stelar tissue in both *Metaxya* and *Lophosoria* (Figs. 10 and 11). A pericycle composed of 1–5 rows of thin-walled parenchyma cells filled with tanniferous substances encircles the primary phloem. Although Ogura (1927, 1938) reported anatomical differences between the proto- and metaphloem in certain squamate species, these two tissues are indistinguishable in the present study. Earlier workers (Schütze, 1906; Ogura, 1927) found that the primary phloem in certain species is composed of distinct rows of sieve cells and phloem parenchyma, but these two cell types are randomly interspersed in *M. rostrata* and *L. quadripinnata*. A similar random arrangement has been noted for certain squamate species (Lucansky, 1976b, 1977). The outermost 1–3 layers of primary phloem in both *Metaxya* and *Lophosoria* are composed of distinctive cells called tangential cells (Figs 10–12), whereas these cells typically occur between the proto- and metaphloem in certain squamate species (Lucansky, 1976b, 1977). These cells represent specialized sieve cells that are devoid of nuclei, possess sieve areas on their lateral walls, and accumulate callose (Sen, 1964), although they have been referred to as false sieve tubes (Schütze, 1906) or as elongated mucilage cells (Ogura, 1927). Although tannin droplets occasionally occur in these cells, they are typically devoid of contents. Previous workers had reported that they contained oil and mucilage (Schütze, 1906; Ogura, 1927). Tangential cells are a characteristic feature of the Cyatheaceae, and have previously been found in certain neotropical squamate species (Lucansky, 1976b, 1977).

The primary xylem in both *Metaxya* and *Lophosoria* consists primarily of tracheids with scalariform pitting, with xylem parenchyma interspersed among these xylary elements. Xylem maturation is mesarch in both genera, with metaxylem tissue comprising the bulk of the xylary mass (Figs. 10 and 11). The cellular



FIGS. 13-18. Anatomical details of tree fern stems. FIG. 13. Pith region of *L. quadripinnata*,  $\times 58$ . Note mucilage-sac cells. FIG. 14. Pith region of *M. rostrata*,  $\times 125$ . FIG. 15. Internal stelar sheath in pith region of *L. quadripinnata*,  $\times 50$ . FIG. 16. Transverse section of adventitious bud of *M. rostrata*,  $\times 118$ . Note sclerified inner cortex. FIG. 18. Transverse section of adaxial petiole strand of *L. quadripinnata*,  $\times 50$ . Note mucilage-sac cells in ground tissue. The abbreviations are: c = cortex, e = endodermis, gt = ground tissue, h = hypodermis, ic = inner cortex, m = mucilage-sac cell, mx = metaxylem, oc = outer cortex, pi = pith, ps = petiole strand, px = protoxylem, pz = parenchymatous zone, s = internal stelar sheath, sg = starch grain, st = sclerenchyma tissue, t = tannins, and vt = vascular tissue.

composition and arrangement of the primary xylem is similar in the squamate genera (Lucansky, 1976b, 1977).

The pith in *Lophosoria* is composed of large, irregularly shaped, thin-walled cells filled with tannins and/or starch grains. Within the pith region of *Lophosoria*, large mucilage-sac cells are randomly distributed, either singly or in groups of 2–10 (Fig. 13), whereas no such cells occur in the pith of *Metaxya* (Fig. 14). Mucilage-sac cells, however, have been reported in the pith region of certain squamate genera of the Cyatheaceae (Lucansky, 1976b, 1977). The pith comprises the bulk of the rhizome in *Metaxya* and consists of thick-walled, variously-shaped parenchyma cells filled with tannins and/or starch grains (Fig. 14). In older rhizomes, these cells become sclerified and closely resemble fibers. An extensive band of sclerified cells in the peripheral region of the pith of *Lophosoria* occurs and constitutes an internal stelar sheath (Fig. 15) which possibly helps to support both the stem and leaves. The thin-walled parenchymatous zone that separates this stelar sheath from the stele may function in the conduction and storage of carbohydrates (Schütze, 1906). Stelar sheaths are a characteristic feature of the Cyatheaceae and have been noted for all advanced neotropical genera (Lucansky, 1974b, 1976b, 1977), yet no sclerified stelar sheaths are found in *Metaxya*. Although the stelar sheaths of the advanced squamate genera are delimited externally and internally by cubical cells (Lucansky, 1976b, 1977), no cubical cells are found between the stelar sheath and pith region in *Lophosoria*. The lack of these distinctive cells may be due to the gradual transition, rather than an abrupt one, from the sclerified cells to the thin-walled cells of the pith. In addition to the stelar sheath, one or more large, localized areas of sclerenchyma tissue frequently occur in the central region of the pith in *Lophosoria*, whereas no sclerenchyma cells occur in the pith region of *Metaxya*. Although no large, sclerified areas occur in the pith region of the squamate genera, numerous small areas do occur (Lucansky, 1974b) and may or may not be associated with medullary bundles (Lucansky, 1976b, 1977). These latter accessory bundles represent another characteristic feature of the Cyatheaceae (Lucansky, 1974b, 1976b, 1977), but they do not occur in either *Metaxya* or *Lophosoria*.

In both *Metaxya* and *Lophosoria*, adventitious buds arise from the rhizome (stem) and occur on the abaxial surfaces of the leaf bases (Figs. 1 and 2). Anatomically these reproductive structures are similar to the stem in each genus, although some differences are noted. The outer boundary of the buds in both genera is a thick-walled epidermis bearing multicellular trichomes. Beneath the epidermis in *Metaxya* is a hypodermis composed of sclerified parenchyma cells (Fig. 16), whereas the hypodermal layer in *Lophosoria* is composed of one (thin-walled or sclerified parenchyma) or two (thin-walled and sclerified parenchyma) layers. The cortex of *Metaxya* consists of thick-walled parenchyma cells filled with tannins, whereas the cortical region in *Lophosoria* is composed of thin-walled parenchyma cells. Mucilage-sac cells are randomly distributed singly or in groups of 2–10 in the hypodermal and cortical regions of *Lophosoria*, but no such idioblasts are found in these tissues in the buds of *Metaxya*. The stelar pattern in the buds of both genera is an amphiphloic siphonostele with no leaf gaps (Fig. 16). The stele is delimited on either side by distinct endodermal layers filled with tanniferous substances. Cellular

composition and arrangement of tissues of the bud stele are similar to those of the stem stele. The pith region of a bud in *Metaxya* consists of either thick- or thin-walled parenchyma cells filled with tannins and starch grains. In *Lophosoria*, the pith consists primarily of thin-walled parenchyma cells, although the central and peripheral zones of this tissue may become sclerified in older buds. Large mucilage-sac cells are also present in the pith of older buds of *Lophosoria*.

Transections of the adventitious roots of both genera show similar anatomical features (*Fig. 17*). The epidermis is typically sloughed off in mature roots, and the outer cortex, composed of thick-walled parenchyma cells, forms the outer boundary of the root. The inner cortex is composed of isodiametric sclerenchymatous fibers and forms the bulk of the cortical zone (*Fig. 17*). A two-zoned cortex is also characteristic of the squamate genera (Lucansky, 1976b, 1977), although other workers found the position of these cell layers reversed in certain species (Schütze, 1906; Sen, 1968). A distinct endodermal layer composed of cells filled with tanniferous substances delimits the stele. A pericycle (1–2 cells thick) composed of large, thin-walled parenchyma cells filled with tannins surrounds the vascular tissue. The primary phloem consists of sieve cells and phloem parenchyma, whereas the primary xylem is composed primarily of scalariform-pitted metaxylem, with some transitional reticulate-to-scalariform and spiral protoxylem noted. The xylem is typically diarch with exarch maturation (*Fig. 17*), although triarch and tetrarch xylem occasionally occur in larger roots of both species.

A single, undivided leaf trace departs from the stem axis in orderly fashion in *Metaxya*, whereas a three-parted trace separates from the stem stele in *Lophosoria* (Lucansky, 1974a). Although Bower (1912) found the leaf trace of *Lophosoria* to be an undivided, single strand that only became divided in larger leaves, the leaf trace is typically three-parted in both small and large leaves.

The petiole strand in *Metaxya* is an undivided, corrugated, horseshoe-shaped structure with distinct lateral folds and inflexed ends, whereas in *Lophosoria* the petiole strand is a three-parted structure consisting of an abaxial arc and an adaxial arc composed of two series (Lucansky, 1974a). The horseshoe-shaped configuration of the petiole strands of both genera show an affinity with both the cyatheoid (Ogura, 1927, 1938; Lucansky & White, 1974) and dicksonioid (Bower, 1913; Holttum & Sen, 1961; Sen, 1968) tree ferns, although the division of the petiole strand of *Lophosoria* anticipates the greater dissection of the strand in the more advanced genera of the Cyatheaceae (Lucansky & White, 1974).

The petiole bases of *Metaxya* and *Lophosoria* are anatomically similar (*Fig. 18*). A single-layered, thick-walled epidermis is persistent in the mature leaves, whereas this epidermal layer is sloughed off in certain squamate genera (Lucansky, 1976b). Beneath the epidermis is a hypodermis composed of sclerified, thick-walled parenchyma cells. In *Lophosoria*, mucilage-sac cells in groups of 2–6 are randomly distributed in this tissue, whereas no such idioblasts are found in the hypodermis of *Metaxya*. The bulk of the petiole in both genera is ground tissue composed of thin-walled parenchyma cells filled with tanniferous substances, although thick-walled parenchyma cells may occur in both genera. Mucilage-sac cells are scattered in this tissue in *Lophosoria* (*Fig. 18*), but are lacking in the ground tissue of



*Metaxya*. Numerous small, intercellular spaces also occur in the ground tissue of both genera. In certain squamate genera, parenchyma cells with tannins or mucilage comprise the ground tissue (Lucansky, 1976b, 1977). The vascular tissue of the petiole in both *M. rostrata* and *L. quadripinnata* is delimited by a distinct endodermis filled with tannins. Cellular composition and arrangement of each petiole strand is similar to the stem stele, except no tangential cells are found in the primary phloem of a petiole. In both species, transitional parenchyma-to-sclerenchyma cells form a sheath on either side of the petiole strands, with the more extensive sheaths towards the center of the petiole base (Fig. 18).

TABLE 1. COMPARATIVE ANATOMICAL AND MORPHOLOGICAL DATA ON *Metaxya*, *Lophosoria* AND THE SQUAMATE GENERA IN THE CYATHEACEAE.

Character	<i>Metaxya</i>	<i>Lophosoria</i>	<i>Squamate Genera</i>
Habit	prostrate rhizome	short, erect stem	arborescent
Hypodermis	single zone	two zones	two zones
Sclerenchyma tissue in cortex and pith	no	yes	yes
Mucilage-sac cells in cortex and pith	no	yes	yes
Cubical cells	no	yes	yes
Tangential cells	yes	yes	yes
Stelar pattern	amphiphloic siphonostele	amphiphloic siphonostele, dictyostele	dicytostele
Stelar sheath	no	yes	yes
Accessory bundles	no	no	yes
Petiole strand	undivided, horseshoe-shaped	divided, horseshoe-shaped	divided, horseshoe-shaped

Previous anatomical and morphological data indicate that *Metaxya* and *Lophosoria* are distinctive and primitive genera, and, in some respects, show an affinity with the dicksonioid tree ferns (Lucansky, 1974a). Gastony and Tryon (1976) also found the spore morphology of these two genera to be distinctive. Gastony (1981, 1982) later reported that the spore morphology of *Metaxya* and *Lophosoria* is similar to certain genera in the Dicksoniaceae, and on the basis of palynological characters. Although similarities exist between *Metaxya* and *Lophosoria*, any relationship between them remains unclear. The present study indicates that significant differences do occur in these two monotypic genera (Table 1), and their affinity with the cyatheoid tree ferns is questionable. Based upon anatomical data, *Lophosoria* is more closely related than *Metaxya* to the squamate genera in the Cyatheaceae, although some similarities to the Dicksoniaceae are noted. A chromosome number  $n=65$  (Walker, 1966) for the genus also shows a relationship to both the cyatheoid and dicksonioid tree ferns. *Metaxya*, on the other hand, is quite distinctive from both *Lophosoria* and the cyatheoid tree ferns and may be better placed in another family or its own family. A chromosome number of  $n=96$  in *Metaxya* (Roy & Holttum, 1965) also supports its isolated position and the segregation of this genus from the family Cyatheaceae.

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#### ALOYSIO SEHNEM (1912—1981)

Aloysio Sehnem was born in Sítio, near Vila Progresso, Brazil, on 24 November 1912, the second son of João Sehnem and Rosa Jungblut. His primary schooling was in Vila Progresso. From 1925 to 1930 he studied at a provincial seminary in São Leopoldo. He joined the Jesuit order as a novice in 1930 and continued his studies in classical languages and philosophy. In 1940 he became a teacher at the Colégio Catarinense de Florianópolis, taught courses in Portuguese and in English, and began his theological studies. He was ordained in 1943, and became a lecturer at the Colégio Santo Inácio de Salvador do Sul, where he rose to the post of Rector (1954-57). Following this, he was a member of the Faculty of Philosophy, Sciences, and Letters at Cristo Rei, which became the Universidade do Vale do Rio dos Sinos (Unisinos), where he taught graduate courses in botany. He was awarded the degree of Livre Docência in November 1974; his thesis was "The ferns of southern Brazil: their ecology, geographical distribution, and routes of migration."

Padre Sehnem's interest in mosses and ferns dated from 1935. During his studies of philosophy and theology, he often collected plants with his colleague Padre Balduino Rambo. His specimens in early years were deposited in the herbarium ASSL at São Leopoldo. Later Padre Sehnem did much to develop the Herbarium Anchieta (PACA), which was founded by Padre Rambo at Porto Alegre but eventually was moved to São Leopoldo. This herbarium concentrates on the fungi and higher plants of southern Brazil, especially of Edo. Rio Grande do Sul. In addition to his work on ferns, which culminated in his publishing almost all the pteridophyte fascicles in Padre Raulino Reitz's "Flora Ilustrada Catarinense," Padre Sehnem was interested in growing prize-winning orchids, and he promoted a number of amateur orchid study groups in southern Brazil.

Padre Sehnem died on 19 March 1981; with his death Brazilian pteridology has suffered a great loss.—*From material provided through the kindness of Dr. Raulino Reitz.*